PRELIMINARY ANALYSES OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, MIGRATIONS, POPULATION STRUCTURE, SURVIVAL AND EXPLOITATION RATES, AND AVAILABILITY AS INDICATED FROM TAG RETURNS

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ABSTRACT

Over 1 million adult Atlantic menhaden, *Brevoortia tyrannus*, were tagged from Long Island Sound to Florida between 1966 and 1969. Tag recoveries indicate these fish migrated northward in spring and early summer and southward in fall. As the fish grew older and larger, they also migrated farther northward each spring. Calculation of rates of interchange between fishing areas indicated that 21% of the recoveries from fish released in Chesapeake Bay in 1967 and 1968 accounted for 72% of the catch of tagged fish 1 yr later in New York and New Jersey.

Preliminary estimates of population parameters were made from tag-recovery and catch data. Survival rates determined yearly from ratio of recoveries, however, varied due to fluctuations in availability. Annual survival rates averaging 0.23 were calculated with Robson-Chapman catch curve analysis and age composition of catch methods. From tag recoveries, exploitation rate was estimated to be 50%, instantaneous fishing mortality rate (F) was 0.95, and instantaneous natural mortality (M) was 0.52. Tag returns also indicated that significant fluctuations in availability of Atlantic menhaden occurred in Chesapeake Bay.

Menhaden, genus *Brevoortia*, are distributed along the Atlantic and Gulf coasts of the United States and constitute the source of the largest U.S. fishery by weight. Prior to 1966 knowledge of population structure and migrations was determined by analysis of meristics, age and size composition and catch-effort data. In the summer of 1966, the Bureau of Commercial Fisheries (now the National Marine Fisheries Service), Beaufort, N.C., began tagging Atlantic menhaden, *Brevoortia tyrannus*, to obtain direct information about population structure, movements, growth, and survival. In 1967, the program was expanded to encompass the Atlantic fishing areas from New York to Florida. Through 1969 a total of 1,066,357 adult menhaden were tagged with an internal ferromagnetic tag and 202,943 were recaptured. In 1969 we began tagging juvenile Atlantic menhaden and adult Gulf menhaden, *B. patronus*, and reduced efforts to tag adult Atlantic menhaden. This paper describes the results of Atlantic menhaden tagging and recovery from 1966 through 1969.

TAGGING METHOD

Preliminary experiments were conducted at the laboratory, Beaufort, to determine the best method of tagging menhaden. After experimenting with several sizes of internal ferromagnetic tags for menhaden larger than 100-mm fork length, we selected a rectangular stainless steel tag with rounded corners, 14.0 by 3.0 by 0.5 mm, identified with a prefix letter and five numbers (Carlson and Reintjes, 1972). From subsequent experiments, Kroger and Dryfoos (1972) found that clean untreated tags were shed less than tags treated with a germicide. Tags were also shed less when inserted anteriorly rather than posteriorly into the body cavity. Tagging guns, manufactured by Bergen-Nautik, a Norwegian firm, were selected over the scalpel-forcep method of insertion because they are safer to use in the field and increase the speed of tagging without increasing mortality or tag shedding.

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Estimates of tagging mortality and tag shedding were also obtained from the experiments. Because these estimates are based on fish acclimated to holding tanks, they are probably minimum estimates of losses experienced in the field. The combined loss was 10 to 20% for menhaden averaging 110 to 160 mm in length. The combined loss for menhaden less than 100 mm was approximately 50%. Most tagging mortality occurred within 3 days and most tag shedding within 2 wk.

A smaller version of the tag was developed for juvenile menhaden. These fish can be tagged most effectively by inserting a 7.0 by 2.5 by 0.4 mm tag posteriorly into the body cavity from the base of the pectoral fin.

The menhaden purse seine fishery provided most of the fish for our work. We also tagged fish obtained from commercial pound nets and our own pound net, purse seines, and haul seines before the purse seine fishery began or where there was no menhaden fishery.

When working with the commercial purse seine fishery, two methods of obtaining and holding fish were used. We accompanied commercial vessels in our own small boats and dipped fish from the purse seine into our holding nets, or we tagged directly from the commercial vessel, keeping the fish alive in holding boxes supplied with flowing seawater. Data were recorded for each group of fish released. A percentage of the fish released were measured to the nearest millimeter and the age determined by counting scale annuli. We recorded the condition of fish, size of catch and time it was made, time tagged fish were released, surface-water temperature, and name of tagger (Pristas and Willis).[2]

TAG RECOVERY

All tags were recovered from menhaden reduction plants because there is no satisfactory way of recovering them from menhaden used for bait or for other reasons precluding their passage through a reduction plant. About 99% of the tags recovered were taken from magnets inside the plants. Primary magnets were placed in the plant's conveyor system between the fish scrap drier and the scrap storage area (Figure 1). About 75% of the tags pass over these magnets the same day the tagged fish are processed. The following day an additional 10% pass the primary magnet. More than 95% of the tags pass the primary magnet within 2 wk from the time they enter the plant. Secondary magnets installed at other locations in the system may not recover tags until months after the fish are landed when the fish scrap is ground into meal or is shipped out of the plant. Whole tagged fish were recovered by using electronic detector-recovery systems which shunted fish past a section of the plant's conveyor. Tagged fish were ejected, and untagged fish continued through processing (Parker, 1972).

Primary and secondary magnets were usually cleaned daily (Parker).[3] Thus, tags recovered on primary magnets indicated the approximate date of capture. Precise recapture locations are not obtained from magnet recoveries, but along the Atlantic coast the fishery in each area was localized and area of recapture could usually be determined.

We tested the efficiency of the recovery system in each plant by putting tags in whole fish in the catch and noting the percentage of these tags recovered. Estimates of the number of tagged fish recaptured were obtained using these primary recovery efficiencies. Tables 1 through 8 give the estimated numbers of tagged fish recaptured by area and season of release and by area and season of recovery. A precise description of tagging and release areas is given in the section on migrations. We estimate that 202,943 tagged fish, or 19% of those released, have been recaptured. Actual recoveries by area and month of release are given by Coston (1971).

MIGRATIONS

We tagged Atlantic menhaden in the estuaries and major fishing areas to test the following

[2] Pristas, P. J., and T. D. Willis. Field tagging methods for menhaden. Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516. Manuscript in preparation.

[3] Parker, R. O., Jr. Magnetic recovery of internal ferromagnetic tags applied to menhaden (*Brevoortia* spp.) Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516. Manuscript in preparation.

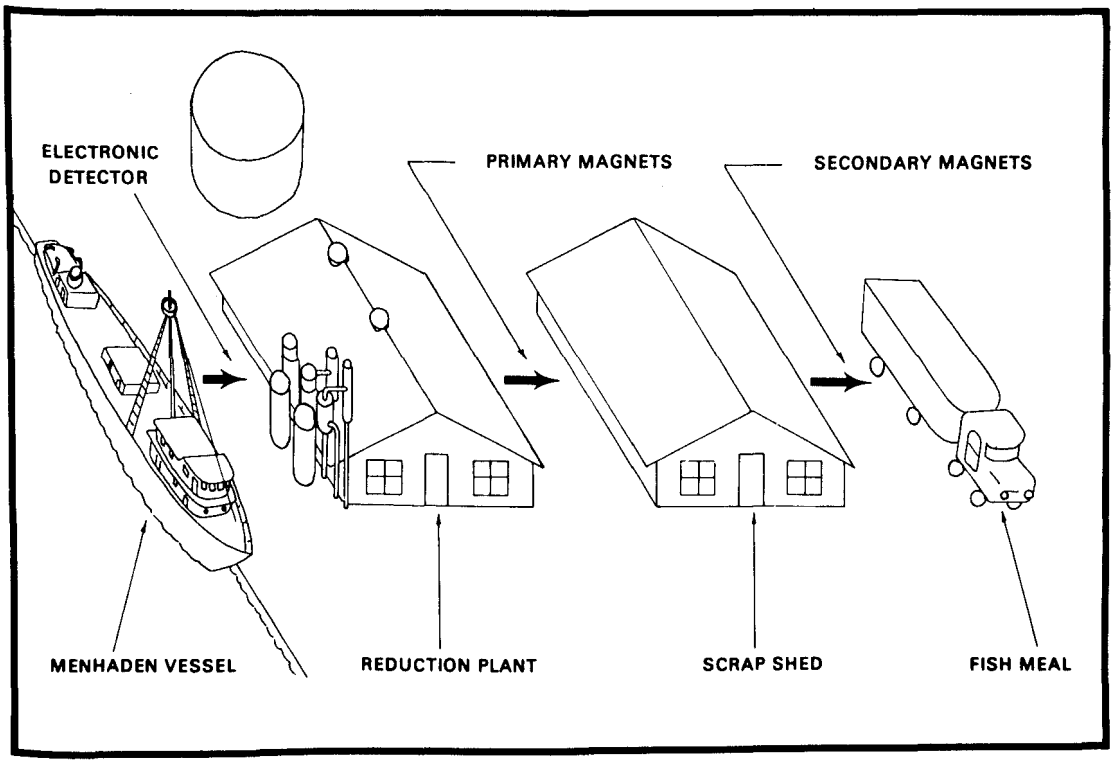

FIGURE 1.—Schematic diagram of a typical menhaden reduction plant showing general areas of tag recovery stations.

hypotheses (first inferred by Roithmayr, 1963):

1. Adult menhaden migrate northward in spring and early summer and southward in fall.
2. Adult menhaden migrate farther northward each spring as they grow larger and older.
3. Juvenile menhaden migrate southward in fall.

The Atlantic coast was divided into five tagging areas based on activities of the commercial fishery (Figure 2). Boundaries between areas are drawn through waters where little fishing occurs, and each area is generally limited to the range of menhaden vessels fishing within that area.

New York Area: Waters along the southern coast of Long Island east of a line due south of Moriches Inlet (lat. 40°46′N and long. 72°44′W), Long Island Sound, and waters northward.

New Jersey Area: Waters north of a line due east of the Maryland-Virginia line (lat. 38°02′N and long. 75°15′W) to the southern boundary of area 1.

Chesapeake Bay Area: Chesapeake Bay proper and coastal waters outside the Bay lying between False Cape, Va., (lat. 36°35′N and long. 75°53′W) and the southern boundary of area 2. Purse seine fishing is prohibited in Maryland waters of Chesapeake Bay.

North Carolina Area: Waters north of a line running due east from the South Carolina-Georgia line at the mouth of the Savannah River (lat. 32°02′N and long. 80°53′W) to the southern boundary of area 3.

Florida Area: Waters south of the southern boundary of area 4.

Our records of the movements of tagged adult menhaden support the above hypotheses. Figure 3 shows the generalized pattern of migration as obtained from tag recoveries.

Northward migration occurs in spring and early summer. Menhaden tagged early in the

TABLE 1.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released in North Carolina in the summer of 1966.
[Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture					Tagged fish recaptured	
			N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.		
	Number		*Number*[2]					*Number*	%
N.C.	74,906	1966 S	*	*	*	5,316	*	5,316	7.1
		F	---	---	*	984	---	984	1.3
		1967 S	---	152	548	138	52	890	1.2
		F	---	---	44	140	---	184	0.2
		1968 S	49	107	229	3	0	388	0.5
		F	---	---	32	107	---	139	0.2
		1969 S	17	13	12	1	0	43	<0.1
		F	---	---	0	21	---	21	<0.1
		Total recaptured						7,965	10.6

[1]S indicates spring and summer; F indicates fall.
[2]* indicates menhaden fishing but no tag recovery was attempted.
-- indicates no menhaden fishing.

TABLE 2.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released in North Carolina in the fall of 1966.
[Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture					Tagged fish recaptured	
			N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.		
	Number		*Number*[2]					*Number*	%
N.C.	21,721	1966 F	--	--	*	424	--	424	2.0
		1967 S	--	79	1,305	131	63	1,578	7.3
		F	--	--	48	124	--	172	0.8
		1968 S	46	146	584	11	3	790	3.6
		F	--	--	41	171	--	212	1.0
		1969 S	11	21	57	0	0	89	0.4
		F	--	--	2	30	--	32	0.1
		Total recaptured						3,297	15.2

[1]S indicates spring and summer; F indicates fall.
[2]* indicates menhaden fishing but no tag recovery was attempted.
-- indicates no menhaden fishing.

fishing season in Florida, North Carolina, and Chesapeake Bay have been recovered in fishing areas north of the release area in the same season of their release. Some fish tagged in Florida in April have been recaptured near Southport, N.C., in May and near Beaufort in June. Few Florida tags were recovered in North Carolina from those released in midseason, and none were recovered in North Carolina from those released late in the season. Menhaden tagged in North Carolina from pound nets early in the spring have been recaptured in pound nets in Chesapeake Bay as early as May and in the purse seine fishery in New Jersey and New York in July. Fish tagged in Chesapeake Bay in April and early May occurred in New Jersey and New York catches as soon as the fisheries began in early June. Again, the amount of movement decreased through the spring, and there appeared to be relatively little movement between fishing areas after June. There appeared to be little northward movement in the spring and early summer of fish tagged in the Maryland portion of Chesapeake Bay. Only a few have been recaptured in New Jersey and none in New York.

Southward migration does not begin until late summer. The North Carolina fall fishery

TABLE 3.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released from New York to Florida in the spring and summer of 1967. [Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture					Tagged fish recaptured	
			N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.		
	Number		*Number*[2]					*Number*	*%*
N.Y.	2,093	1967 S	--	270	0	0	0	270	12.9
		F	--	--	0	58	--	58	2.8
		1968 S	134	68	3	1	0	206	9.8
		F	--	--	0	4	--	4	0.2
		1969 S	14	31	0	0	0	45	2.2
		F	--	--	0	2	--	2	0.1
			Total recaptured					585	28.0
N.J.	13,660	1967 S	--	1,313	17	0	0	1,330	9.7
		F	--	--	139	863	--	1,002	7.3
		1968 S	102	423	247	6	0	778	5.7
		F	--	--	26	126	--	152	1.1
		1969 S	14	46	7	1	0	68	0.5
		F	--	--	5	9	--	14	0.1
			Total recaptured					3,344	24.4
Chesapeake Bay	100,128	1967 S	--	360	13,770	0	0	14,130	14.1
		F	--	--	1,419	2,944	--	4,363	4.4
		1968 S	691	3,533	11,480	10	0	15,714	15.7
		F	--	--	849	3,212	--	4,061	4.1
		1969 S	158	517	810	21	0	1,506	1.5
		F	--	--	0	505	--	505	0.5
			Total recaptured					40,279	40.3
N.C.	112,428	1967 S	--	35	1,221	12,522	0	13,778	12.3
		F	--	--	133	7,553	--	7,686	6.8
		1968 S	16	523	2,664	832	46	4,081	3.6
		F	--	--	317	1,418	--	1,735	1.5
		1969 S	27	106	281	21	0	435	0.4
		F	--	--	0	148	--	148	0.1
			Total recaptured					27,863	24.7
Fla.	95,832	1967 S	--	0	0	425	5,958	6,383	6.7
		F	--	--	0	0	--	0	0
		1968 S	0	128	626	596	477	1,827	1.9
		F	--	--	70	381	--	451	0.5
		1969 S	0	25	102	18	9	154	0.2
		F	--	--	0	47	--	47	<0.1
			Total recaptured					8,862	9.4
Combined	324,141	1967 S	--	1,978	15,008	12,947	5,958	35,891	11.1
		F	--	--	1,691	11,418	--	13,109	4.0
		1968 S	943	4,675	15,020	1,445	523	22,606	7.0
		F	--	--	1,262	5,141	--	6,403	2.0
		1969 S	213	725	1,200	61	9	2,208	0.7
		F	--	--	5	711	--	716	0.2
			Grand total recaptured					80,933	25.0

[1]S indicates spring and summer; F indicates fall.
[2]-- indicates no menhaden fishing.

TABLE 4.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released in North Carolina in the fall of 1967.
[Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture					Tagged fish recaptured	
			N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.		
	Number		*Number*[2]					*Number*	*%*
N.C.	38,920	1967 F	--	--	0	5,188	--	5,188	13.3
		1968 S	213	725	1,662	538	172	3,310	8.5
		F	--	--	185	909	--	1,094	2.8
		1969 S	46	87	268	39	0	440	1.1
		F	--	--	2	127	--	129	0.3
			Total recaptured					10,161	26.0

[1]S indicates spring and summer; F indicates fall.
[2]-- indicates no menhaden fishing.

TABLE 5.—Estimated number of tagged fish recaptured, by area and season, from Atlantic menhaden released from New York to Florida in the spring and summer of 1968.
[Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture					Tagged fish recaptured	
			N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.		
	Number		*Number*[2]					*Number*	*%*
N.Y.	2,370	1968 S	344	200	0	0	0	544	23.0
		F	--	--	0	10	--	10	0.4
		1969 S	35	72	5	0	0	112	4.7
		F	--	--	0	20	--	20	0.8
			Total recaptured					686	28.9
N.J.	21,789	1968 S	321	5,460	18	0	0	5,799	26.6
		F	--	--	188	970	--	1,158	5.3
		1969 S	68	311	57	4	0	440	2.0
		F	--	--	0	85	--	85	0.4
			Total recaptured					7,482	34.3
Chesapeake Bay	132,596	1968 S	10	144	26,822	0	0	26,976	20.3
		F	--	--	2,076	7,525	--	9,601	7.2
		1969 S	158	410	3,333	63	0	3,964	3.0
		F	--	--	38	1,611	--	1,649	1.2
			Total recaptured					42,190	31.7
N.C.	103,483	1968 S	3	25	643	13,070	0	13,741	13.3
		F	--	--	150	1,575	--	1,725	1.7
		1969 S	3	41	1,003	482	5	1,534	1.5
		F	--	--	11	400	--	411	0.4
			Total recaptured					17,411	16.9
Fla.	118,295	1968 S	0	0	0	1,498	10,994	12,492	10.6
		F	--	--	3	61	--	64	<0.1
		1969 S	0	21	495	1,732	329	2,577	2.2
		F	--	--	0	162	--	162	0.1
			Total recaptured					15,295	13.0
Combined	378,533	1968 S	678	5,829	27,483	14,568	10,994	59,552	15.7
		F	--	--	2,417	10,141	--	12,558	3.3
		1969 S	264	855	4,893	2,281	334	8,627	2.3
		F	--	--	49	2,278	--	2,327	0.6
			Grand total recaptured					83,064	21.9

[1]S indicates spring and summer; F indicates fall.
[2]-- indicates no menhaden fishing.

TABLE 6.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released in North Carolina and Florida in the fall of 1968.
[Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture					Tagged fish recaptured	
			N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.		
	Number		*Number*[2]					*Number*	*%*
N.C.	6,937	1968 F	--	--	0	480	--	480	6.9
		1969 S	16	25	184	99	0	324	4.7
		F	--	--	2	72	--	74	1.1
		Total recaptured						878	12.7
Fla.	524	1968 F	--	--	0	0	--	0	0
		1969 S	0	0	0	0	0	0	0
		F	--	--	0	0	--	0	0
		Total recaptured						0	0
Combined	7,461	1968 F	--	--	0	480	--	480	6.4
		1969 S	16	25	184	99	0	324	4.3
		F	--	--	2	72	--	74	1.0
		Grand total recaptured						878	11.7

[1]S indicates spring and summer; F indicates fall.
[2]-- indicates no menhaden fishing.

TABLE 7.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released from New York to Florida in the spring and summer of 1969.
[Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture					Tagged fish recaptured	
			N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.		
	Number		*Number*[2]					*Number*	*%*
N.Y.	8,468	1969 S	1,310	301	0	0	0	1,611	19.0
		F	--	--	0	419	--	419	4.9
		Total recaptured						2,030	23.9
N.J.	700	1969 S	2	7	0	0	0	9	1.3
		F	--	--	0	2	--	2	0.3
		Total recaptured						11	1.6
Chesapeake Bay	75,581	1969 S	0	0	4,261	0	0	4,261	5.6
		F	--	--	54	1,875	--	1,929	2.6
		Total recaptured						6,190	8.2
N.C.	24,685	1969 S	0	0	98	2,429	0	2,527	10.2
		F	--	--	7	529	--	536	2.2
		Total recaptured						3,063	12.4
Fla.	108,150	1969 S	0	0	0	117	4,828	4,945	4.6
		F	--	--	--	4	--	4	0.0
		Total recaptured						4,949	4.6
Combined	217,584	1969 S	1,312	308	4,359	2,546	4,828	13,353	6.1
		F	--	--	61	2,829	--	2,890	1.3
		Grand total recaptured						16,243	7.4

[1]S indicates spring and summer; F indicates fall.
[2]-- indicates no menhaden fishing.

TABLE 8.—Estimated number of tagged fish recaptured, by area and season, from adult Atlantic menhaden released in North Carolina in the fall of 1969.
[Estimates based on primary magnet tag recoveries.]

Tagging area	Tagged fish released	Recovery season[1]	Area of recapture					Tagged fish recaptured	
			N.Y.	N.J.	Chesapeake Bay	N.C.	Fla.		
	Number		*Number*[2]					*Number*	*%*
N.C.	3,091	1969 F	--	--	0	402	--	402	13.0

[1] F indicates fall.
[2] -- indicates no menhaden fishing.

begins in November and, as the season progresses, fish tagged in more northern areas enter the fishery. The first recoveries from releases of the previous summer are from fish tagged in North Carolina. Then fish from Virginia, Maryland, Delaware, and New Jersey enter the North Carolina fishery before the end of November. During the first week of December, tags are recovered from fish tagged in Long Island Sound. In 1969 we tagged as far north as Narragansett Bay, R.I., and tags from that area were not recovered in the fall fishery before December 18. Consequently, it appears that the fish enter the North Carolina fall fishery progressively; those from farther north enter last.

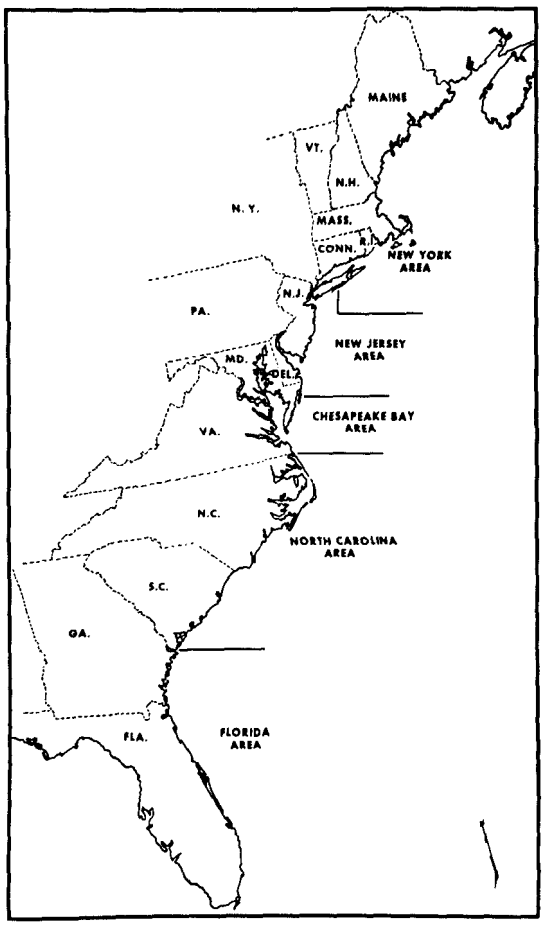

FIGURE 2.—Commercial fishing areas for Atlantic menhaden along Atlantic coast of the United States.

Rates of interchange between fishing areas can be inferred from recoveries of the 1967 and 1968 releases. Two important aspects of interchange between areas have been considered: 1) where did tagged fish recaptured in a particular area come from, and 2) where did fish released in a particular area go?

To determine the relative contributions of fish from one area to another, it is necessary to either tag in proportion to abundance (with equal tagging survival rates in each area) or to adjust the returns to compensate for disproportionate tagging in the different areas. In general we attempted to tag in proportion to abundance, but in practice this is impossible since relative abundances are not known until after the fact of tagging. Consequently, we have attempted to adjust the returns in relation to the achieved density of tags in each area.

There are several possible approaches to equalizing tag density (number of tags per million individual fish landed) in the different areas. We examined three approaches for the 1967 spring and summer tagging season:

1. Season-average density: Total number of recoveries from fish re-

leased within the area and season divided by total number of individual fish landed within the area and season.

2. Maximum-monthly density: Highest monthly ratio of number of recoveries from releases within the area and season to the total number of individual fish landed during the month.

3. Last-month-of-season density: Number of recoveries during the last month of fishing from releases within the area and season divided by the total number of individual fish landed during the month.

If the areas were truly closed to recruitment, immigration and emigration, and if there were rapid dispersal of tagged fish throughout the population in each area, any one of these approaches would provide adequate density indices.

We observed that the maximum density was not always achieved at the end of the season and believe that the effects of recruitment and migration near the end of the fishing season confound the third approach. We believe that selecting the month with the highest density may also be misleading due to nonrandom distribution of tags within each area. We selected the season average as a robust statistic for determination of an index of achieved tag density.

After obtaining the index of density (the season-average density) for each area, we determined the standardization factor necessary for each area to achieve an arbitrarily selected

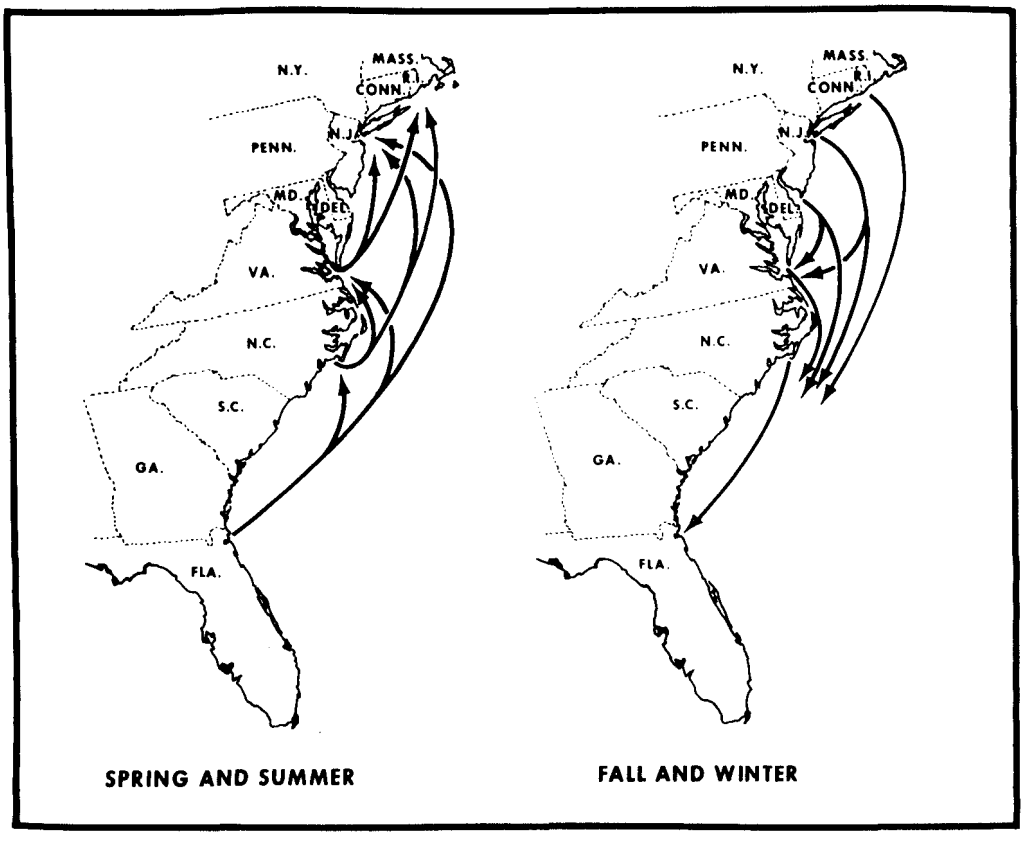

FIGURE 3.—Generalized movements of tagged Atlantic menhaden.

density of 50 tags per million individual fish (Table 9). Multiplying the number of recaptures in subsequent fishing season by the appropriate standardization factor will equalize tag densities from each tagging area so that meaningful comparisons can be made of the relative contribution of fish from different areas in succeeding seasons.

Fish tagged in Chesapeake Bay and the Florida areas contributed most to landings in other areas (Table 10). In New York and New Jersey, 83.2% of the 1968 tag recoveries came from fish tagged in Chesapeake Bay in 1967. In Chesapeake Bay, 85.6% of the 1968 recoveries were from fish tagged in that area in 1967. Fish tagged in Florida the previous year made up 75.3% of the recoveries in North Carolina and 97.9% of the recoveries in Florida. The pattern of migration was similar for fish tagged in 1968 and recaptured in 1969 (Table 11).

Selection of either of the other two alternative approaches for determining the index density for each area had little effect in changing the relative contributions from the different areas. Table 12 shows the differences in relative contributions from spring and summer releases recaptured in 1968.

We have determined the destination of fish tagged in each area based on the distribution of recoveries in successive summers. The adjustments of ratios do not in any way affect this analysis. These percentages are based upon the numbers of recaptures in the different areas from all the releases in an area. For example, Table 3 and Table 10 show that of the fish tagged in Florida in 1967 and recaptured in the summer of 1968, 26% were recovered in Florida, 33% in North Carolina, 34% in Chesapeake Bay,

TABLE 9.—1967 adjustments of tags per million individual fish landed to achieve equal density of tags (50 tags per million individual fish) in each area.

Area	Tags recaptured (within season and area) *a*	Individual fish caught *b*	*a*/*b*	Standardization factor
	Number	*No.* × 10^6		
North & Middle Atlantic	1,583	32	49.5	1.01
Chesapeake Bay	13,770	410	33.6	1.49
North Carolina	12,522	118	106.1	0.47
Florida	5,958	256	23.3	2.15

TABLE 10.—Calculated numbers of tags recovered and percentage distributions for 1967 summer releases recovered in summer 1968.

Tagging area	Standardization factor	Recovery area: N.Y. and N.J.	Chesapeake Bay	N.C.	Fla.	Total
		Number[1]				
N.Y. and N.J.	1.01	734	252	7	0	993
Chesapeake Bay	1.49	6,294	17,105	15	0	23,414
N.C.	0.47	253	1,252	391	22	1,918
Fla.	2.15	275	1,346	1,281	1,026	3,928
Total		7,556	19,955	1,694	1,048	30,253
Distribution of recoveries by area of recovery (where tagged fish came from).						
		Percent				
N.Y. and N.J.		9.7	1.3	0.4	0	
Chesapeake Bay		83.2	85.6	0.9	0	
N.C.		3.4	6.4	23.4	2.1	
Fla.		3.6	6.7	75.3	97.9	
Distribution of recoveries by area of release (where tagged fish go).						
		Percent				
N.Y. and N.J.		73.8	25.4	0.7	0	
Chesapeake Bay		26.9	73.0	0.1	0	
N.C.		13.2	65.3	20.4	1.1	
Fla.		7.0	34.2	32.6	26.1	

[1] Adjusted numbers from Table 3.

TABLE 11.—Calculated numbers of tags recovered and percentage distributions for summer 1968 releases recovered in summer 1969.

Tagging area	Standardization factor	Recovery area: N.Y. and N.J.	Chesapeake Bay	N.C.	Fla.	Total
		Number[1]				
N.Y. and N.J.	0.54	262	33	2	0	297
Chesapeake Bay	0.85	483	2,833	54	0	3,370
N.C.	0.88	39	883	424	4	1,350
Fla.	0.84	18	416	1,455	276	2,165
Total		802	4,165	1,935	280	7,182
Distribution of recoveries by area of recovery (where tagged fish came from).						
		Percent				
N.Y. and N.J.		32.5	0.8	0.1	0	
Chesapeake Bay		60.4	68.0	2.8	0	
N.C.		4.9	21.3	22.0	1.5	
Fla.		2.2	10.0	75.2	98.5	
Distribution of recoveries by area of release (where tagged fish go).						
		Percent				
N.Y. and N.J.		88.2	11.2	0.6	0	
Chesapeake Bay		14.3	84.1	1.6	0	
N.C.		2.9	65.4	31.4	0.3	
Fla.		0.8	19.2	67.2	12.8	

[1] Adjusted numbers from Table 5.

TABLE 12.—Comparison of percentage distributions of recoveries by area of recovery (where fish came from) calculated from three different indices of achieved density of tagging. Method 1 is based on season-average density; Method 2 on maximum-monthly density; Method 3 on last-month-of-season density. Data are for spring and summer 1967 releases recaptured in spring and summer 1968.

Tagging area	Recovery area: New York and New Jersey			Chesapeake Bay			North Carolina			Florida		
	Method 1	2	3	1	2	3	1	2	3	1	2	3
New York and New Jersey	10	20	8	1	3	1	<1	4	4	0	0	0
Chesapeake Bay	83	79	91	86	93	98	1	4	11	0	0	0
North Carolina	3	1	<1	6	2	1	23	26	23	2	3	2
Florida	4	1	<1	7	2	<1	75	67	61	98	97	98

and 7% in New York and New Jersey. These data are not adjusted for different exploitation rates in the different areas; however, we believe the basic pattern would not change with adjustment.

These data point up the importance of fish from Chesapeake Bay. An average of 21% of the recoveries 1 yr later from fish released in Chesapeake Bay in 1967 and 1968 occurred in the New York and New Jersey areas. Thus 21% of the fish from the Bay made up 72% of the total catch of tagged fish in the New York and New Jersey areas. The patterns of movement observed for 1967 and 1968 releases are similar. In the second year after release, there is even more northward displacement from each tagging area (Table 13).

Peak migration speeds estimated from one area to another along the coast ranged from 11 to 16 km/day. A fish tagged off St. Augustine, Fla., in April traveled to Beaufort in no more than 53 days or 14 km/day. The shortest migration time from Chesapeake Bay to New Jersey in the spring was 29 days or 11 km/day.

TABLE 13.—Calculated numbers of tags recovered and percentage distributions for summer 1967 releases recovered in summer 1969.

Tagging area	Standardization factor	Recovery area: N.Y. and N.J.	Chesapeake Bay	N.C.	Fla.	Total
		Number[1]				
N.Y. and N.J.	1.01	105	7	1	0	113
Chesapeake Bay	1.49	1,006	1,207	31	0	2,244
N.C.	0.47	63	132	10	0	205
Fla.	2.15	54	219	39	19	331
Total		1,228	1,565	81	19	2,893
Distribution of recoveries by area of recovery (where tagged fish came from).						
		Percent				
N.Y. and N.J.		8.6	0.5	1.8	0	
Chesapeake Bay		81.9	77.1	38.2	0	
N.C.		5.1	8.6	12.7	0	
Fla.		4.4	13.8	47.3	100	
Distribution of recoveries by area of release (where tagged fish go).						
		Percent				
N.Y. and N.J.		92.2	6.5	1.3	0	
Chesapeake Bay		44.8	53.8	1.4	0	
N.C.		30.2	64.7	5.0	0	
Fla.		16.4	65.9	11.8	5.9	

[1] Adjusted numbers from Table 3.

In the fall the shortest migration time from the Chesapeake Bay to Cape Hatteras, N.C. was 25 days indicating a rate of 12 km/day. A fish tagged near Fire Island Inlet on the south side of Long Island, N.Y., in October was recaptured near Cape Hatteras 41 days later. This fish traveled at a rate of 16 km/day. There was no apparent difference in maximum rates of travel between spring and fall migrations.

Juvenile menhaden were first tagged in Rhode Island in October 1969. Of 1,020 juveniles tagged, 3 have been recovered in North Carolina and 1 in Florida as of July 1970 (Kroger, Dryfoos, and Huntsman, 1971). The first North Carolina recovery was in January 1970 during the fall fishery, and the remaining recoveries were in June 1970. The lone Florida recovery was in July 1970.

In general our recoveries of tagged fish support all three hypotheses: Adult menhaden migrate northward in spring and early summer and southward in fall, and menhaden migrate farther northward as they grow older. Juveniles also migrate southward in fall.

POPULATION STRUCTURE

Previous conjecture by Hildebrand (1948) and from work based on morphology of Atlantic menhaden by June (1958), Sutherland (1963) and June (1965), summarized by Reintjes (1969), led to the conclusion that at least two subpopulations occur along the coast, one north of Long Island and one to the south. Nicholson (1972a) differed with previous interpretations of the morphometric data and has presented an alternative interpretation suggesting a single population.

Recoveries of tagged fish also indicate that Atlantic menhaden constitute a single population. Adult fish tagged in Florida, North Carolina, Cheapeake Bay, and New Jersey have been recovered north of the release sites in subsequent years. Fish tagged in each area during the summer have subsequently been recovered in the North Carolina fall fishery. Juvenile menhaden tagged north of Long Island show a southward displacement from their estuarine rearing areas. The pattern of recoveries suggests an intermingling and mixing of menhaden from various areas during the winter and a resegregating by size during the following spring and summer. This inference also agrees with previous analyses of changes in age and size distribution (Nicholson, 1971a). All recent work has tended to negate the existence of a

hypothetical northern subpopulation. Tagging of known sexually active fish in the north in the spring or summer followed by their recapture in the North Carolina fall fishery, where they could be assumed to be sexually active again, would confirm this conclusion. For the present, with such significant mixing of fish from the various areas, the Atlantic menhaden resource should be considered as one population.

SURVIVAL AND EXPLOITATION RATES

Tag recoveries can provide estimates of survival and exploitation rates that are independent of those obtained from catch and effort data (Widrig, 1954), and with such data can provide measures of changes in resource availability. Estimates of annual survival rates were calculated for releases of each season by determining the ratio of recoveries in successive years. These estimates vary considerably because of fluctuations in availability. Survival rates also were obtained using the Robson-Chapman catch curve analysis (Paulik, 1962). The latter rates for the entire recovery period were the most consistent (Table 14). Better estimates of survival rates will be possible when we have a longer series of recovery data. Survival rates based on analyses of the age composition of the catch for 1966 to 1968 average 0.22 and are in good agreement with the average estimate of 0.24 from tag returns. Using an average value of 0.23 corresponds to a total instantaneous mortality rate of $Z = 1.47$.

Exploitation rates can be obtained from the estimated percentage of tags recaptured from early season releases after corrections are made for tagging mortality and tag shedding (Table 15). Tagging mortality and shedding losses for 1967-69 are thought to be about 10% for New York and New Jersey, 20% for Virginia, 25% for North Carolina, and 40% for Florida releases. The differences in percentage result primarily from differences in fish size. The average exploitation rate along the Atlantic coast, weighted by the catch in numbers of fish and preliminary estimates of tagging mortality, varied between 42 and 54%. Estimates for 1967 and 1968 from North Carolina fall fishery releases agree with values obtained from the weighted average summer releases. This indicates that most menhaden occurring in the fall fishery also occur within the fishery during the summer. The best single estimate of exploitation rate obtained from these tagging data is 50%.

Fishing and natural mortality rates can be obtained from exploitation rates and total mortality rates. Using our estimates of the instan-

TABLE 15.—Exploitation rate by area and year of release.

Release area	Year of release		
	1967	1968	1969
New York	33.6	47.1	55.7
New Jersey	52.9	52.9	--
Chesapeake Bay	48.2	65.4	21.7
North Carolina	33.5	49.1	57.6
Florida	66.7	33.3	32.0
Average (weighted by catch)	49.3	53.9	41.8
North Carolina fall fishery	42.9	48.0	--

TABLE 14.—Survival rates for all releases by season and by year, 1966-69.

Releases	Annual survival rates[1]					Robson-Chapman annual survival rate[2]
	Fall 67/66	Summer 68/67	Fall 68/67	Summer 69/68	Fall 69/68	
1966						
Summer	0.187	0.436	0.755	0.111	0.151	0.23
Fall	--	0.501	1.232	0.113	0.151	.33
1967						
Summer	--	--	0.488	0.098	0.112	.37
Fall	--	--	--	0.133	0.118	.13
1968						
Summer	--	--	--	--	0.185	.15
Average	0.187	0.468	0.825	0.114	0.143	.24

[1] Survival rate is ratio of recoveries in either fall or summer fishery 1 yr to recoveries in the same season the previous year.
[2] Robson-Chapman annual survival rate calculated from combined summer and fall recoveries. For fall releases recoveries were only considered for subsequent summer and fall seasons.

taneous total mortality rate (Z = 1.47) and exploitation rate (μ = 0.50), the instantaneous fishing mortality rate (F) is calculated to be 0.95 and the natural mortality rate (M), 0.52. Each year 50% of the fish in the fishery are being caught and 24% are dying from natural causes. This estimate of rate of fishing is in general agreement with the others based on an analysis of the catch and effort data in earlier years (Schaaf and Huntsman, 1972) at a higher level of fishing effort. We are continuing to analyze and to add additional years of data to reduce the effects of fluctuating availability upon the estimates.

AVAILABILITY

Tagging studies suggest that in Chesapeake Bay there are significant fluctuations in availability of Atlantic menhaden within and between years. Since most of the summer catch of Atlantic menhaden is landed in Chesapeake Bay (60% to 75%, 1967 through 1970) and since our movement data suggest that in the summer the stocks in different areas are relatively stable, we made a special study of the fluctuations in availability there. Fluctuations in availability may be caused by factors making the fish more or less accessible, such as weather and horizontal or vertical distribution of the fish or by differences in vulnerability brought about by changes in fish behavior, gear selectivity, or numbers of fish (Cushing, 1968). Murphy (1966) developed a population model for the Pacific sardine, incorporating the idea of variation in availability. In his model:

$$\frac{N_i + 1}{N_i} = e^{-M-(rvf)_i} = S_i$$

where

N_i is the number of fish present in the population in years;
e is the base of the natural logrithms;
M is the instantaneous natural mortality rate;
f is fishing effort;
r is an index of availability;
v is a residual constant; and
S_i is the annual survival rate of the population.

As Murphy indicated, errors in measuring f also contribute to r but in the menhaden fishery in Cheasapeake Bay we use a vessel week as the unit of effort (Nicholson 1971b), and there is little error in this measurement.

The factor v includes changes in vessel efficiency or fishing power which are separable from effects of availability. Schaaf and Huntsman (1972) concentrate on changes in the catchability coefficient (rv) resulting from changes in vessel efficiency and changes in distribution of effort. Over a number of years and major fishing innovations, efficiency of the vessels has increased markedly. However, for the limited number of years in our analysis (1967-70) and in consideration of only the Chesapeake Bay area, we believe it is reasonable to assume that unit efficiency and consequently v, may be considered constant. The quantity rv is a variable catchability coefficient and, since v is assumed constant, relative estimates of r can be obtained from the percentage of tags recaptured per unit of fishing effort (Gulland, 1963).

Fluctuations in availability, or percent tag recaptures per unit of fishing effort, in Chesapeake Bay were observed in 1967 through 1970. Estimates in 1970 were even more striking than those obtained in the earlier years. The data used for this analysis are based upon tags released during the first 2 wk of the purse seine fishery in Chesapeake Bay by our best taggers. The number of tags released varied by year, i.e., 1967, 4,290 tags; 1968, 10,387 tags; 1969, 2,147 tags; and 1970, 21,189 tags. Table 16 shows the actual and relative values, compared with the base year 1967, of catch, effort, catch per unit effort (CPUE), percent recapture, availability index, and population size. The percentage of tagged fish recaptured, shown in Table 16, is not comparable to the exploitation given for Chesapeake Bay in Table 15 because no adjustment was made in Table 16 for tagging mortality and tag shedding which we assume to be constant each year, nor were recoveries considered at plants outside of Chesapeake Bay during the summer or fall. Consequently, the data shown in Table 16 for population size are relative estimates and cannot be considered true estimates of the number of fish. Table 16 shows that while the CPUE increased almost

TABLE 16.—Actual and comparative values of catch, effort, catch per unit effort (CPUE), percent recapture, availability index and population size for menhaden landings in Chesapeake Bay, 1967-70 using 1967 as the base year. (Comparative values are in parentheses.)

Year	Catch (Millions of individual fish) C	Effort (Number of vessel weeks) f	CPUE C/f	Percent recaptured R	Availability index R/f	Population size $100\ C/R$
1967	384 (1.00)	757 (1.00)	0.507 (1.00)	24.1 (1.00)	0.0318 (1.00)	1,593 (100.)
1968	449 (1.17)	601 (0.79)	0.747 (1.47)	34.3 (1.42)	0.0571 (1.80)	1,309 (82.)
1969	255 (0.66)	519 (0.69)	0.491 (0.97)	14.3 (0.59)	0.0276 (0.87)	1,783 (112.)
1970	791 (2.06)	501 (0.66)	1.579 (3.11)	45.8 (1.90)	0.0914 (2.87)	1,727 (108.)

threefold between 1969 and 1970, the availability index more than tripled, so the difference in the population size was relatively small. Table 16 suggests that most of the variation in catch during 1967-70 in Chesapeake Bay results from the reduction in effort and the fluctuations in availability rather than actual changes in fish abundance.

Anomalies in survival rates calculated from tagged fish or age composition data provide another indication of fluctuation in availability. When availability is high and a larger than normal catch is made, a correspondingly large number of fish are recaptured. Then, compared to a normal year, the survival rate is overestimated when the high number is the numerator and underestimated when it is the denominator. Such an anomaly was noted in our estimates of survival rate based on tag recoveries and also in age composition data for Chesapeake Bay in the summer of 1968 (Henry, 1971).

Differences in monthly catches between 1967 and 1968 from June to September also suggest changing rates of availability. The catch for these months in 1968 was up to 28% over the previous year, but nearly three-fourths of the difference occured in July. Most of these fish were caught near the Maryland border in the vicinity of Tangier Island. Since the time and location of large catches was so restrictive, the large catch probably resulted from fish moving from Maryland to Virginia, rather than a general increase in the number of fish in the Bay.

Vulnerability appears to have varied in recent years in Chesapeake Bay. The proportion of the weekly catch made on Mondays in Chesapeake Bay has increased since 1962, coinciding with an increase in fishing effort in the early 1960's and a decrease in relative abundance during the decade (Nicholson, 1972b). Although this phenomenon had not generally been observed in other areas, it demonstrates one type of fluctuation in availability.

SUMMARY

From 1966 through 1969, over 1 million adult Atlantic menhaden were tagged in the major fishing areas from Long Island Sound to Florida. We estimate that more than 200,000 tags have been recaptured.

Tag recoveries demonstrate a seasonal migration of menhaden along the coast: Northward in spring and early summer and southward in fall. As the fish grow older and larger they migrate farther northward each spring. Maximum migration speeds from one area to another along the coast vary from 11 to 16 km/day.

Rates of interchange between fishing areas were determined from recoveries of the 1967 and 1968 releases. An important feature of the data is that 21% of the recoveries from fish released in Chesapeake Bay in 1967 and 1968 occurred off the coasts of New York and New Jersey 1 yr later. These fish from Chesapeake Bay made up 72% of the catch in New York and New Jersey.

Preliminary estimates of population parameters were made from tag-recovery data. Survival rates were estimated by several methods; i.e., ratio of recoveries in successive years, Robson-Chapman catch curve analysis technique, and age composition of catch for 1966 to 1968. Rates determined yearly from ratio of recoveries varied due to fluctuations in availability. Annual survival rates were based upon Robson-Chapman catch curve analysis and age composition of catch. Both use several years data and agree closely, averaging 0.23. Better

estimates of survival rates will be possible when a longer series of recovery data is available.

Exploitation, fishing, and natural mortality rates are estimated from tag recaptures. The best estimate of exploitation rate from these data is 50%. Instantaneous fishing mortality rate (F) is estimated to be 0.95 and instantaneous natural mortality (M) is 0.52.

Tagging studies suggest that there are significant fluctuations in availability of Atlantic menhaden in Chesapeake Bay.

LITERATURE CITED

CARLSON, F. T., AND J. W. REINTJES.
1972. Suitability of internal tags for Atlantic menhaden. Fish. Bull., U.S. 70:514-517.

COSTON, L. C.
1971. Summary of tags released and recovered for the Atlantic menhaden, 1966-69. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Data Rep. 66, 117 p. on 2 microfiche.

CUSHING, D. H.
1968. Fisheries Biology; a study in population dynamics. Univ. Wis. Press, Madison, 200 p.

GULLAND, J. A.
1963. The estimation of fishing mortality from tagging experiments. Int. Comm. Northwest Atl. Fish., Spec. Publ. 4:218-227.

HENRY, K. A.
1971. Atlantic menhaden *(Brevoortia tyrannus)* resource and fishery—analysis of decline. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-642, 32 p.

HILDEBRAND, S. F.
1948. A review of the American menhaden, genus *Brevoortia*, with a description of a new species. Smithson. Misc. Collect. 107(18):1-39.

JUNE, F. C.
1958. Variation in meristic characters of young Atlantic menhaden, *Brevoortia tyrannus*. Cons. Per. Int. Explor. Mer, Rapp. P.-V. Réun. 143:26-35.
1965. Comparison of vertebral counts of Atlantic menhaden. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish 513, 12p.

KROGER, R. L., AND R. L. DRYFOOS.
1972. Tagging and tag-recovery experiments with Atlantic menhaden, *Brevoortia tyrannus*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-664, 11 p.

KROGER, R. L., R. L. DRYFOOS, AND G. R. HUNTSMAN.
1971. Movement of juvenile Atlantic menhaden tagged in New England waters. Chesapeake Sci. 12:114-115.

MURPHY, G. I.
1966. Population biology of the Pacific sardine *(Sardinops caerulea)*. Proc. Calif. Acad. Sci., Ser. 4, 34:1-84.

NICHOLSON, W. R.
1971a. Coastal movements of Atlantic menhaden as inferred from changes in age and length distributions. Trans. Am. Fish. Soc. 100:708-716.
1971b. Changes in catch and effort in the Atlantic menhaden purse-seine fishery 1940-68. Fish. Bull., U.S. 69:765-781.
1972a. Population structure and movements of Atlantic menhaden, *Brevoortia tyrannus*, as inferred from back calculated length frequencies. Chesapeake Sci. 13:161-174.
1972b. Fishing pressure and its influence on Monday catches of Atlantic menhaden in the Chesapeake Bay purse-seine fishery. Chesapeake Sci. 13:215-218.

PARKER, R. O., JR.
1972. An electronic detector system for recovering internally tagged menhaden genus *Brevoortia*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-654, 7 p.

PAULIK, G. J.
1962. Use of the Chapman-Robson survival estimate for single-and-multi-release tagging experiments. Trans. Am. Fish. Soc. 91:95-98.

REINTJES, J. W.
1969. Synopsis of biological data on the Atlantic menhaden, *Brevoortia tyrannus*. U.S. Fish Wildl. Serv., Cir. 320, 30 p.

ROITHMAYR, C. M.
1963. Distribution of fishing by purse seine vessels for Atlantic menhaden, 1955-59. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 434, 22 p.

SCHAAF, W. E., AND G. R. HUNTSMAN.
1972. Effects of fishing on Atlantic menhaden stock: 1955-1969. Trans. Am. Fish. Soc. 101: 290-297.

SUTHERLAND, D. F.
1963. Variation in vertebral numbers of juvenile Atlantic menhaden. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 435, 21 p.

WIDRIG, T. M.
1954. Method of estimating fish populations, with application to Pacific sardine. U.S. Fish Wildl. Serv., Fish. Bull. 56:141-166.